Scale and Benthic Composition Effects on Biomass and Trophic Group Distribution of Reef Fishes in American Samoa[1]

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Abstract: We determined spatial patterns in distribution and biomass of 163 fish species in nearshore waters around Tutuila Island, American Samoa. Visual surveys of reef fishes along 30 by 5 m belt transects were conducted using a hierarchical nested design at five spatial scales from individual transects to tens of kilometers, allowing assessment of broad geographic patterns. Benthic cover data were derived from video transect surveys to test the relationship between habitat and distributions of reef fishes. We found that fish biomass, density, and numerical abundance in American Samoa are dominated by herbivores from relatively few species in the families Acanthuridae and Scaridae. Subsets of carnivore species covaried positively with live coral, algae, and coralline algae cover. Herbivores, in contrast, covaried positively with filamentous algae and coralline algae (i.e., their foods). Biomass of fishes at different trophic categories was associated with higher abundance of food material and habitat availability. Significantly higher biomass occurred along the south shore of Tutuila and at reefs with greater exposure to wave energy, such as topographic points, despite the occurrence of lower live coral cover. Significant variations in fish biomass occurred at large spatial scales, specifically at habitat and exposure levels. Variations at these scales were apparently driven by association of the most dominant trophic group with its food source and the extent but not the quality of habitat.

UNDERSTANDING COMPLEX systems such as coral reefs is challenging, especially if patterns and processes act simultaneously at various spatial and temporal scales. Scaling up patterns observed at small scales could lead to flawed conclusions when extrapolated to larger scales (Syms 1995, Edmunds and Bruno 1996, Hughes et al. 1999, Miller et al. 2000). However, generalizations from small-scale patterns have been made up to the scale of 200 m^2 (Chittaro 2004). Ecological data, especially for reef fishes, are more meaningful if surveys are designed to cover scales relevant to the organism (Sale 1998). Scaling is particularly important when studying organisms whose distributions are tightly coupled with the structuring forces acting at multiple spatial and temporal scales (Hewitt et al. 1998).

The distribution patterns of organisms are rarely random: often, underlying processes create patterns at different scales. For example, reef fish distributions at the Great Barrier Reef followed a wave exposure gradient (Victor 1986, Gust et al. 2001), whereas those at the Gulf of California and Indian Ocean responded to spatial variations in various habitat parameters at scales of tens of kilometers (Aburto-Oropeza and Balart 2001, Garpe and Ohman 2003). Variations in distribution patterns due to habitat variables have been attributed to resource partitioning (Eagle et al. 2001), shelter (Syms 1995), and utilization characteristics (Garcia-Charton and Perez-Ruzafa 2001) of reef fishes.

Utilizing the advantages of spatial scaling in the analysis of biomass and abundance of

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reef fishes may help put conclusions into a more useful management context. Variations in species-abundance distribution for corals and fishes are affected by environmental stochasticity occurring at a particular spatial scale (Connolly et al. 2005). Management intervention should, therefore, be robust to encompass a spectrum of environmental variability to which managed organisms are exposed and to ensure niche similarity (Pandolfi 2002). Distribution patterns of organisms at large spatial scales (hundreds of kilometers) reflect variation in history, dispersion, and regional processes, and disturbance plays a major role at small scales (Pandolfi 2002). Scaling was also used in the management (specifically the zoning strategy) of the Florida Reef Track (Murdoch and Aronson 1999, Miller et al. 2000). The presence of large-scale variations, however, highlights the importance of careful selection of sampling scale, design, and interpretation of monitoring data (Edmunds and Bruno 1996).

We incorporated scaling in our sampling design because our objective was to elucidate patterns of distribution of fish assemblages across spatial scales of the entire island of Tutuila relative to the benthos and habitat distribution. This has been done previously for benthic communities in the Caribbean and Florida Reef Track (Hughes 1994, Klein and Orlando 1994). Our aim was to determine how fish biomass of targeted fish species varied at different spatial scales and identify possible mechanisms that cause such patterns. Furthermore, we aimed to determine possible predictive factors that may drive the distribution pattern using benthic assemblages as habitat and food-source parameters. This will provide information on how the fish community around a small South Pacific island such as Tutuila is distributed, which could help in developing management strategies for conservation.

MATERIALS AND METHODS

Study Site

This study was conducted in American Samoa, located at approximately 14° 20′ S and 170° 44′ W (Figure 1). It comprises five volcanic islands (Tutuila, Aunu'u, Ofu, Olosega, and Ta'u) and two atolls (Rose and Swains Atoll). There are two extensive banks (Taema and Nafanua) located at the southeastern side of the Tutuila Island. Due to logistic and time constraints, this study was conducted only at the main island of Tutuila, which is the center of the territory where 97% of the population resides. Most of the villages are found along the coastline, with the population concentrated at the inner bay areas.

Sampling Design

The sampling design followed a modified nested hierarchical design (Figure 2) in which Tutuila was categorized into two exposures (northern and southern exposures, which are actually the cartographic sides of the island covering tens of kilometers) accounting for various levels of wave intensity due to swells generated by the trade winds (Friedlander et al. 2003). These variations in wave intensity were based on current marine data from the Ocean Weather Inc. Web site (www.oceanweather.com), accounts from local experts, and long-term personal observations. The north shore of Tutuila is exposed to more-intense wave action generated by stronger wind coming from the northwesterly trades occurring from January to March. That is also the hurricane season, when storm-generated waves reach up to 4–5 m high. The north shore could therefore be considered as more exposed to high-intensity waves. A period of calm weather on both sides of the island occurs between April and June. The southeast trade winds occur from July to December, characterized by a continuous low-intensity wind generating moderate wave action. Nafanua and Taema Banks provide some sheltering for the southeastern half of the island, where the wave energy is attenuated before breaking at the shoreline.

Within each exposure, the island was further subdivided into two strata: the eastern and western sectors. This accounted for the longitudinal variations in exposure due to the island's topographic and geomorphic characteristics. The southwestern side of Tutuila is

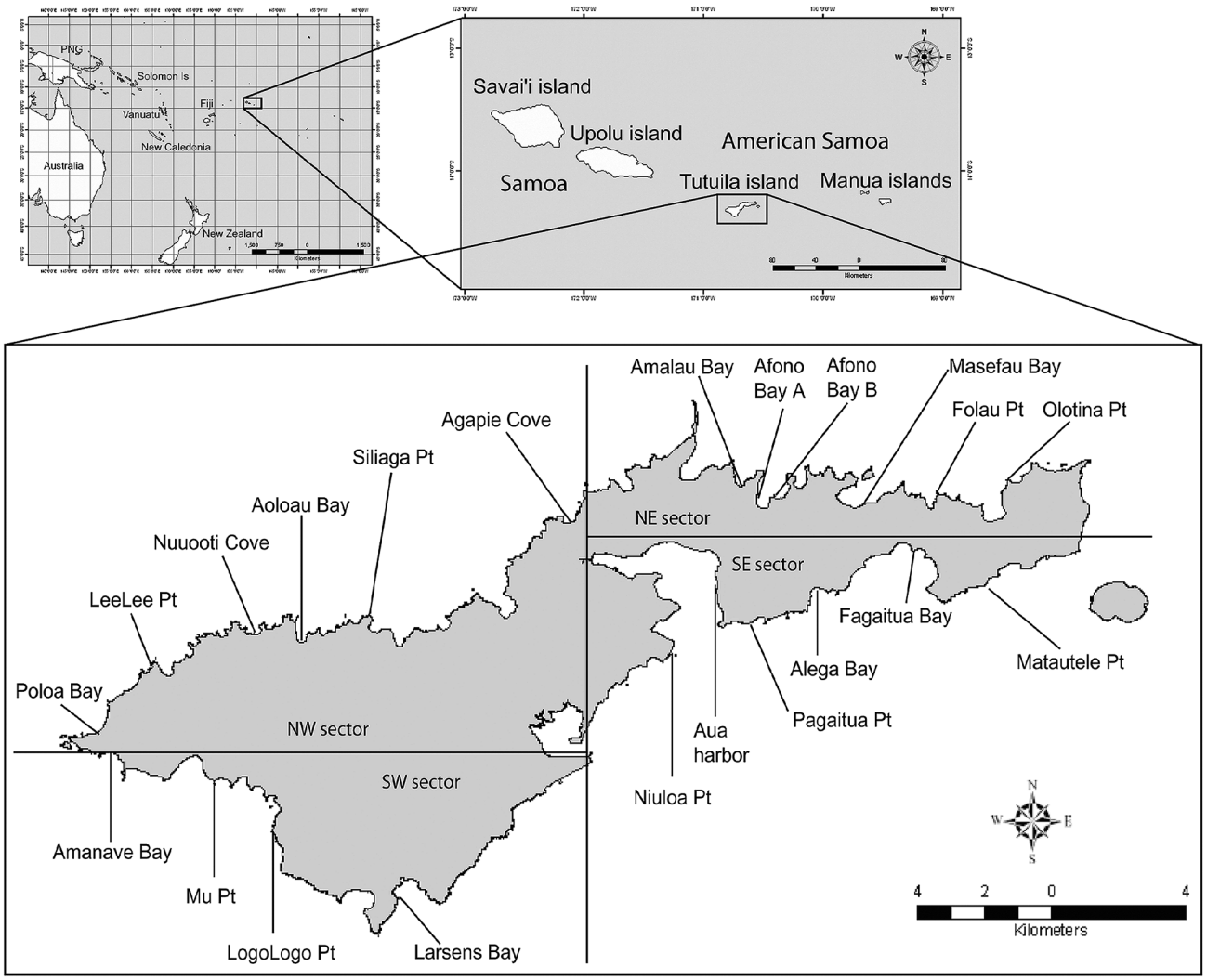

FIGURE 1. Location map of the American Samoa Archipelago showing the main island of Tutuila, with 22 permanent monitoring sites.

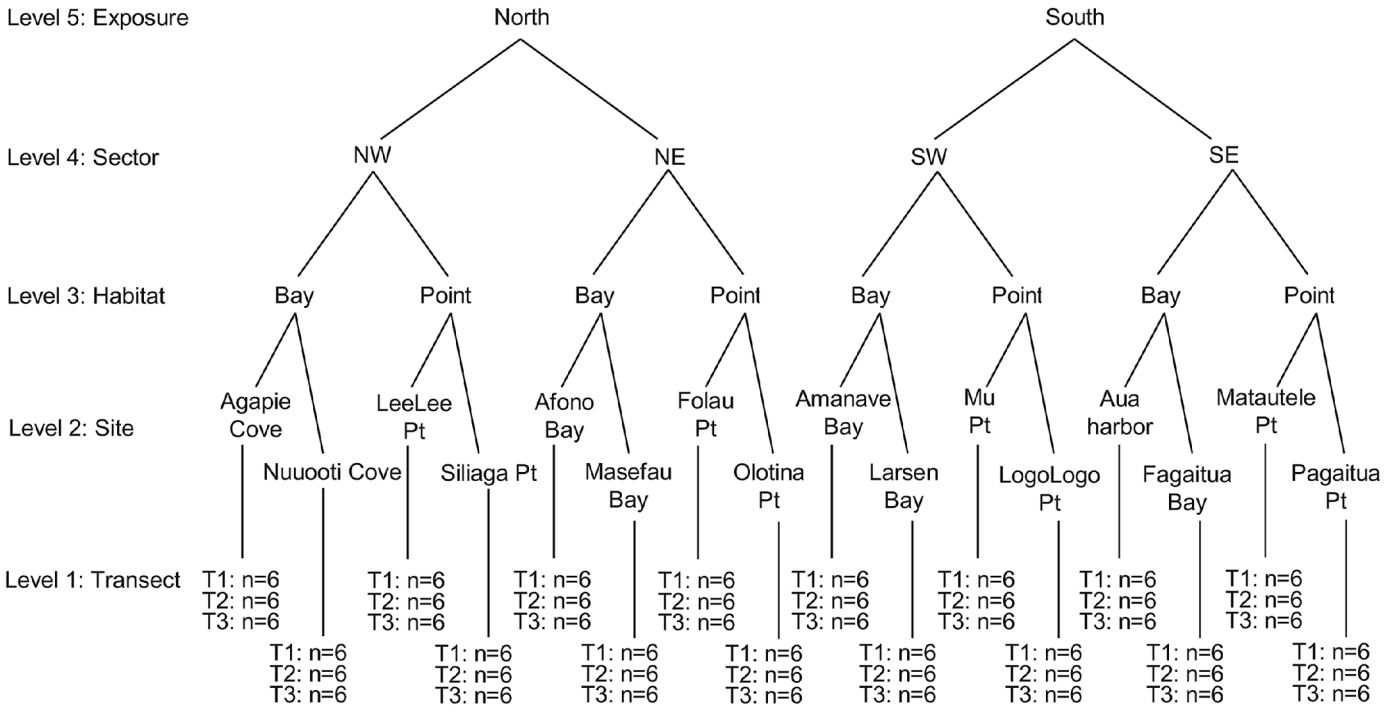

FIGURE 2. Hierarchical nested sampling scheme of the fish visual census survey. Twenty-two sites were assessed, but only 16 were randomly included in the analysis to satisfy the balanced requirement of analysis of variance with nested design. n = number of subsampling plot within each transect.

acutely angled, resulting in further sheltering from the southeasterly trade winds.

Each sector was subdivided into two habitat types: embayment and point habitats (covering a scale of thousands of meters). Point habitats were reef areas located at the topographic tips of the island. These were considered to be more exposed than embayment reef habitats that were found well inside the bays. Each habitat type had two to four replicate sites (covering hundreds of meters), and each site had three to five replicate transects (at a scale of tens of meters). A total of 22 sites was surveyed, but the data were truncated randomly to 16 sites (two on each habitat type per sector) and three replicate transects in each site to achieve a balanced design. Several runs of the analysis with different combinations of sites generally yielded similar results.

Field Survey Methods

This study was focused only on coral reef fishes that are being utilized for subsistence and recreational fishing (targeted species). A species list was generated from the Western Pacific Fishery Information Network database to determine which species were being caught locally. A total of 163 species was extracted. The survey was conducted from July to December 2005 during the prevalence of the southeast trades. Surveys were done between 0900 and 1400 hours, thereby recording only diurnal assemblages. Approximately four replicate 30-m transects were laid by the first diver on the reef slope at 10-m depth. This zone was selected because it was present at all sites and was where a majority of the representative families of targeted species were found. Fish visual census (FVC) using belt transects was conducted by the second diver at 22 permanent monitoring sites around Tutuila Island. The diver waited 15 min before starting the survey to allow the fish community to revert to its normal behavior. A 5 by 5 m sampling area was used at every transition point (every 5 m) in each transect. Two randomization schemes were used to achieve independence in sampling. The first was at the 5 by 5 m sampling area, where the diver randomly selected which side of the transect tape to do the counts (5 m left or right of the tape or at the middle 2.5 m on each side). The second was at the transect level, where the distance between transects was assigned randomly for each replicate within and between sites. Only snapshots of the fish assemblage found within the sampling area were recorded. Any fish that swam in was recorded as off-count and was not included in the analysis. The total length (nearest centimeter) and number of all targeted species were estimated visually. The biomass of each fish recorded was computed by converting length data to weight using the allometric length-weight conversion: $W = aL^b$, where parameters a and b were constants for the allometric growth equation from FishBase (www.fishbase.org). Length (L) was expressed in centimeters and weight (W) in grams. Biomass was expressed per unit area (g/m^2) and converted to metric tons per square kilometers (mt/km^2). The mean total biomass (sum of biomass values of all species within transects averaged among replicate transects) was computed to summarize values on a site level.

Benthic community surveys were also carried out by another diver after the visual fish counts at the same transects. A diver swam slowly (7 min per 30-m transect) and recorded the substrate and associated benthic community using an underwater video camera. Footages were taken 0.5 m above the substrate with the camera positioned perpendicular to the benthos. Footages were digitized using Pinnacle Studio v.8.3.17 (Pinnacle Systems 2002), and "still-frames" (photos) were grabbed using VirtualDub 1.6.0 (Lee 2002). At least 50 frames per transect were grabbed to maximize spatial coverage and minimize frame overlaps. Percentage cover data were extracted from the photos using Coral Point Count with Excel Extensions v.3.0 (Kohler and Gill 2006). Substrate identifications were summarized to general categories such as hard coral, soft coral, other fauna, abiotic, coralline algae, and fleshy/filamentous algae. The percentage cover per

TABLE 1

Top 20 Dominant Key Reef Species in the 22 sites (74 transects) Surveyed in Tutuila Island

Family	Species Name	Trophic Guild	Frequency	Biomass	IRD
Acanthuridae	*Ctenochaetus striatus*	Herbivore	100.00	21.85	2185.01
Acanthuridae	*Acanthurus nigricans*	Herbivore	92.77	7.58	703.58
Scaridae	*Chlorurus japanensis*	Herbivore	77.11	4.72	363.81
Acanthuridae	*Naso lituratus*	Zooplanktivore	56.63	2.73	154.76
Scaridae	*Chlorurus sordidus*	Herbivore	65.06	2.13	138.74
Lethrinidae	*Monotaxis grandoculis*	Carnivore	48.19	2.52	121.51
Scaridae	*Scarus rubroviolaceus*	Herbivore	36.14	3.26	117.96
Acanthuridae	*Acanthurus lineatus*	Herbivore	42.17	2.74	115.40
Scaridae	*Chlorurus frontalis*	Herbivore	15.66	7.35	115.17
Scaridae	*Scarus oviceps*	Herbivore	34.94	2.51	87.58
Serranidae	*Cephalopholis urodeta*	Carnivore	68.67	1.27	87.19
Scaridae	*Scarus forsteni*	Herbivore	26.51	2.98	79.03
Balistidae	*Melichthys vidua*	Omnivore	51.81	1.46	75.87
Lutjanidae	*Macolor niger*	Zooplanktivore	26.51	1.97	52.26
Serranidae	*Cephalopholis argus*	Carnivore	50.60	0.82	41.38
Caesionidae	*Pterocaesio tile*	Zooplanktivore	10.84	3.53	38.28
Scaridae	*Scarus psittacus*	Herbivore	27.71	0.74	20.52
Acanthuridae	*Zebrasoma scopas*	Herbivore	33.73	0.59	19.99
Scaridae	*Scarus globiceps*	Herbivore	18.07	1.10	19.93
Scaridae	*Scarus frenatus*	Herbivore	20.48	0.95	19.49

Note: Species are ordered according to decreasing index of relative dominance (IRD).

life-form, category, and transect variance was automatically generated by the program. The cover data of live coral, fleshy/filamentous algae, and coralline algae were averaged within sites.

Data Analysis

The biomass contribution of individual species was expressed as a percentage of total biomass. This showed which species contributed most to the targeted species biomass. Index of relative dominance (Friedlander et al. 2003) was used to describe which species dominate the reef as a function of frequency of sighting and biomass contribution (percentage frequency detected within transect × percentage biomass contribution).

A square-root transformation satisfied the homoscedasticity requirement of parametric statistics (Sokal and Rohlf 1995). Analysis of variance with hierarchical nesting design was used to detect differences in biomass at various nesting levels (Choat and Ayling 1987, Underwood 1997). The nesting levels incorporated the spatial scaling from exposure down to transect level, where the smallest scale was nested within the next larger spatial scale. A similar procedure was used for the substrate data.

Factor analysis was used to reduce the number of variables and to detect structure in the species composition among sites. Fish density data were used for these analyses using trophic guilds (FishBase: www.fishbase.org) as grouping variables. Correlation coefficients were used to evaluate relationships between species under each factor group. Data were log transformed and rotated using normalized varimax. Factor scores were assigned to each case based on the factor loadings, and multiple regression was used to determine responses of each factor to the covariates live coral, macroalgae, and coralline algae cover. Only results from carnivores and herbivores were described because other trophic groups had shown no significant association with any of the covariates.

The Statistica 6.0 (StatSoft, Inc. 2001) statistical package was used for all analyses.

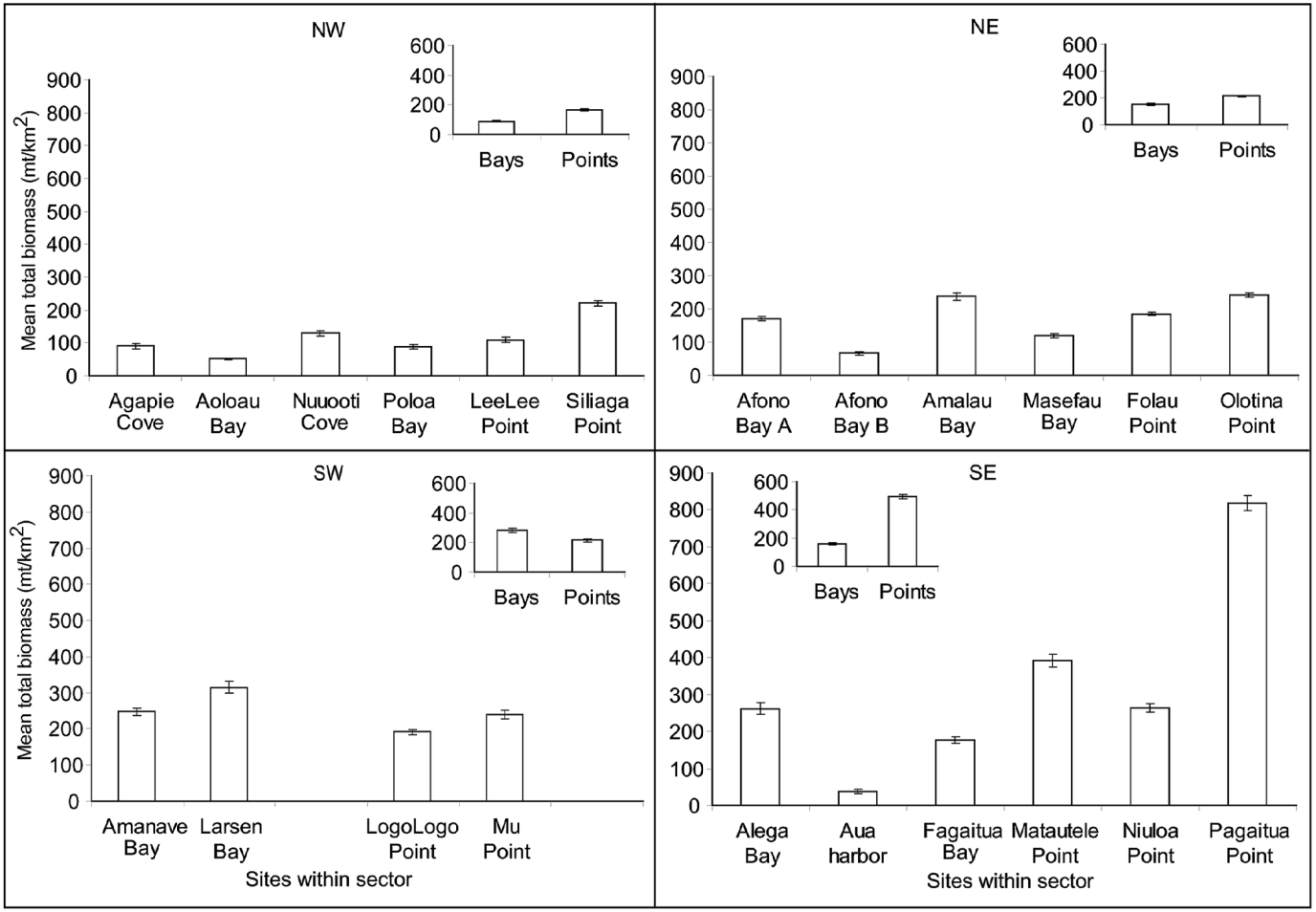

FIGURE 3. Mean biomass of key reef species among sites nested within habitats. Habitat is nested within sector (individual box). Each sector is nested within exposure (northern exposures, *top;* southern exposures, *bottom*). Inset graphs are averaged biomass by habitat types. Only 16 out of 22 sites were used for the statistical analysis (see Figure 2 caption).

RESULTS

Fish Assemblage Composition

The targeted species assemblage was dominated by Acanthuridae (Table 1). The brown bristletooth surgeonfish (*Ctenochaetus striatus*) occurred in 100% of all transects and accounted for 22% of total biomass. The second most dominant was the whitecheek surgeonfish (*Acanthurus nigricans*), contributing to 8% of total fish biomass. Other common species were bigeye emperor (*Monotaxis grandoculis*), black snapper (*Macolor niger*), two small grouper species (*Cephalopholis argus* and *C. urodeta*), and pinktail triggerfish (*Melichthys vidua*). The most abundant parrotfishes were *Chlorurus japanensis* and *C. sordidus*. The redlip parrotfish (*Scarus rubroviolaceus*) was the third most dominant and third highest in biomass among herbivores. The top parrotfish, in terms of biomass, was the tanface parrotfish (*Chlorurus frontalis*) because they were often sighted as terminal-phase adults in schools.

Herbivores dominated the trophic groups and accounted for 66% of biomass, and carnivores made up 16% of the total fish biomass. Zooplankton feeders were the third dominant trophic group, composing 13% of the total biomass due to abundance of bluestreak fusilier (*Pterocaesio tile*), and omnivores composed only 5% of the total fish biomass.

Biomass of Targeted Species across Spatial Scales

The biomass of targeted species varied greatly among sites, with mean values ranging from 37 mt/km^2 in Aua inside the harbor to 819 mt/km^2 in Pagaitua Point (Figure 3). The high value at Pagaitua Point was due to large schools of surgeonfish (*C. striatus* and *Acanthurus blochii*), parrotfish (*C. sordidus* and *C. japanensis*), and fusiliers (*P. tile*). Large redlip parrotfish (*S. rubroviolaceus*) contributed 47% of the average biomass at this site. Aua had the lowest biomass due to low abundance of fish composed mostly of small *C. striatus*.

There were no apparent patterns when comparing between sites due to high fluctuations in biomass values at an overall level (Figure 3). Higher spatial scale comparisons indicated significantly higher biomass at point areas than at embayment areas within sectors (three out of four cases [$F = 6.59$; $df = 2,319$; $P < .01$]) (Figure 3 insets, Table 2). There was no significant variation in biomass moving longitudinally from east to west ($F = 0.29$; $df = 2,319$; $P = .75$). The south shore of Tutuila had significantly higher biomass than the north shore. Significant variations in biomass occurred across different habitats and exposure levels ($F = 10.51$; $df = 1,319$; $P < .01$).

TABLE 2

Analysis of Variance with Hierarchical Nested and Univariate Design Testing for Variations in Mean Fish Biomass across Spatial Scales

Effects	SS	df	MS	*F*	*P*
Exposure	**85.23**	**1**	**85.23**	**10.51**	**.00**
Sector (Exposure)	4.76	2	2.38	0.29	.75
Habitat (Sector)	**106.90**	**2**	**53.45**	**6.59**	**.00**
Site (Habitat)	0.00	2	0.00	0.00	1.00
Transect (Site)	16.39	4	4.10	0.51	.73
Error	2586.15	319	8.11		

Note: Results with significant effects are in **boldface**.

Benthic Composition and Species Association

Benthic composition varied across space. On a large scale, there appeared to be more live coral cover at the north shore of Tutuila than the south shore, but this difference was not significant ($F = 0.36$; $df = 1,319$; $P = 0.55$) (Figure 4, Table 3). Most reef areas at the north shore were concentrated within sheltered bay areas characterized by high live coral cover. Point areas, however, were mostly volcanic pavement with a high cover of coralline algae and low cover of live corals. The benthic composition at the south shore, however, had a different spatial pattern, with bays having lower live coral cover and reefs extending to the farthest topographic point, which had slightly higher live coral cover. Both habitats were dominated by coralline algae. Most of the fleshy/filamentous algae were present at the north shore.

The trophic structure of the targeted fish

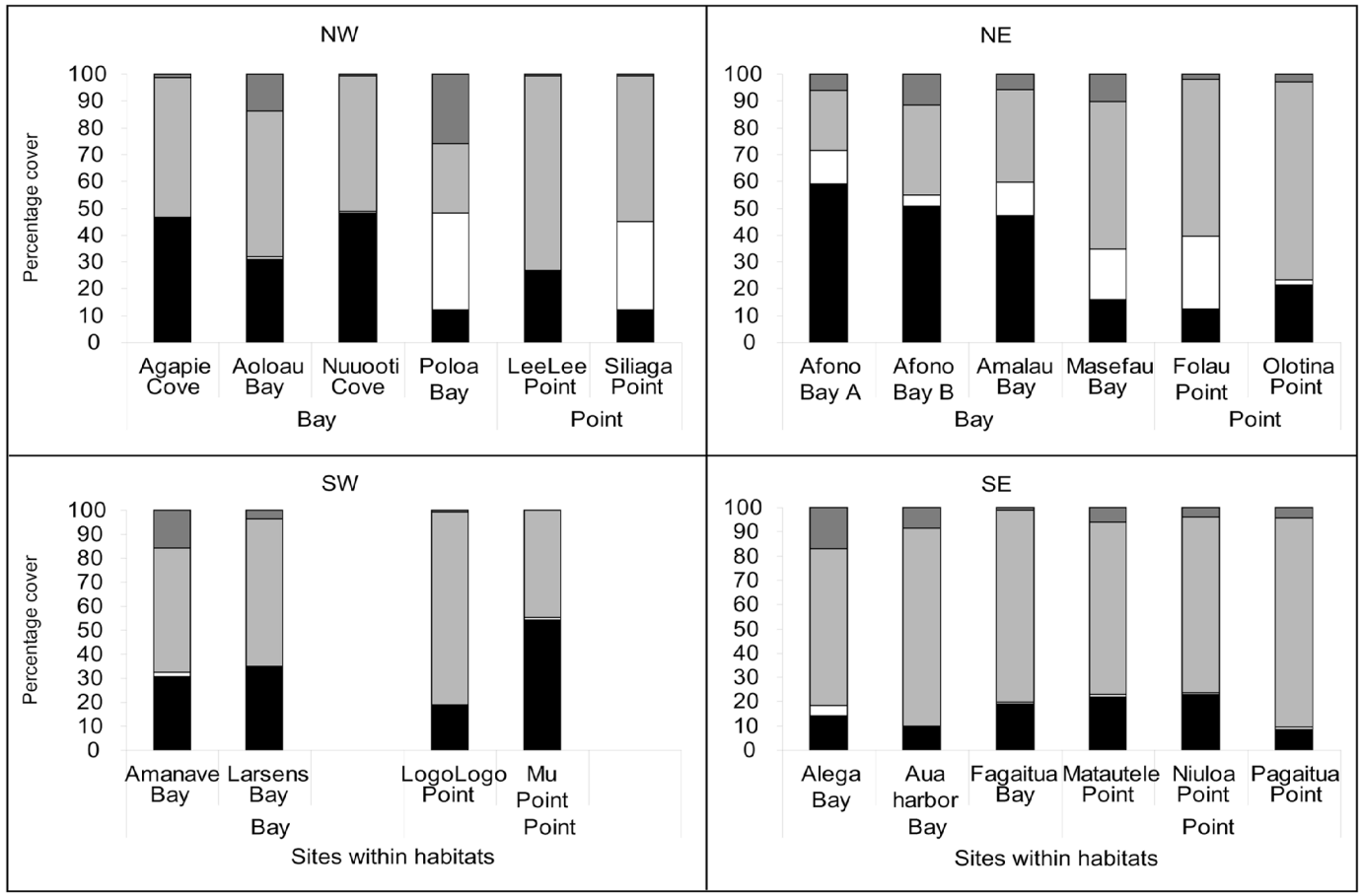

FIGURE 4. Percentage cover of live corals, fleshy/filamentous algae, coralline algae, and other benthic components at various sites within each habitat type per sector. (Black, live coral cover; white, fleshy/filamentous algae; light gray, coralline algae; dark gray, other benthic components.)

TABLE 3

Analysis of Variance with Hierarchical Nested Design Testing for Variations in Live Coral Cover across Spatial Scales

Effects	SS	df	MS	*F*	*P*
Exposure	1.01	1	1.01	0.36	.55
Sector (Exposure)	**191.92**	**2**	**95.96**	**34.26**	**.00**
Habitat (Sector)	**210.70**	**2**	**105.35**	**37.62**	**.00**
Sites (Habitat)	**61.18**	**2**	**30.59**	**10.92**	**.00**
Transect (Site)	10.68	4	2.67	0.95	.43
Error	907.38	324	2.80		

Note: Results with significant effects are in **boldface**.

community was characterized by fewer carnivores than herbivores, in terms of both numerical abundance and biomass (Figures 5 and 6, respectively). The highest number of carnivores was found in Agapie Cove, with a total of 194 individuals/600 m^2 dominated by flagtail grouper (*C. urodeta*) and yellowspot emperor (*Gnathodentex aureolineatus*). Biomass, on the other hand, was highest in Niuloa Point due to presence of large bigeye emperor (*M. grandoculis*) and dogtooth tuna (*Gymnosarda unicolor*). The highest herbivore abundance was found at Matautele Point, with 965 individuals/600 m^2 dominated by brown bristletooth (*C. striatus*) and whitecheek surgeonfish (*A. nigricans*), but biomass was highest at Pagaitua Point due to dominance of larger herbivores (i.e., *S. rubroviolaceus* and *C. japanensis*). Zooplanktivores were abundant at Larsens Bay, Pagaitua, and Matautele Point (394, 320, and 238 individuals/600 m^2, respectively) primarily due to bluestreak fusiliers (*P. tile*). Zooplanktivore biomass followed a similar pattern of abundance except at Amanave Bay, where biomass was high due to large individuals of black triggerfish (*Melichthys niger*).

Factor and regression analyses revealed that live coral cover explained 69.9% of the variance in abundance of carnivore species. Among the carnivore species, only squaretail grouper (*Plectropomus areolatus*), redspot emperor (*Lethrinus lentjan*), and lyretail grouper (*Variola louti*) had significant positive association with live coral cover (Table 4). The bigeye emperor (*M. grandoculis*), snappers (*Lutjanus monostigma* and *Aphareus rutilans*), and slingjaw wrasse (*Epibulus insidiator*) were positively associated with fleshy/filamentous and coralline algae cover.

Herbivores showed no significant association with live coral cover but had significant positive association with fleshy/filamentous and coralline algae cover (Table 5). Five species of parrotfish (*Scarus forsteni*, *S. rivulatus*, *S. niger*, *S. oviceps*, and *C. japanensis*) and three species of surgeonfish (*Acanthurus olivaceus*, *A. nigrofuscus*, and *C. striatus*) showed a significant correlation with fleshy/filamentous algae. *Hipposcarus longiceps* and *Scarus ghobban* had significant correlations with live coral and coralline algae cover, which was unexpected because of their ecological or trophic characteristics.

DISCUSSION

Spatial Patterns: Biomass and Habitat Relationship

We found significant variation in fish biomass across spatial scales. Higher total biomass of the targeted species was found at exposed point areas than at sheltered embayment areas. Furthermore, biomass of the targeted species depended on exposure regimes and abundance of coral reef habitats. A similar pattern was found at the Great Barrier Reef, where exposed areas had higher biomass and abundance of parrotfish (Williams 1982, Gust et al. 2001). This was in contrast with the main Hawaiian Islands, where areas exposed to wave action had lower biomass than sheltered areas, probably due to seasonal storm surges and variability in environmental conditions that severely disturb fish populations as well as the benthos, resulting in low habitat complexity and dominance of encrusting corals (Friedlander et al. 2003).

Several studies have shown higher biomass and abundance of reef fishes in areas with greater habitat complexity (i.e., coral reefs with high coral cover) (McClanahan 1994, Ohman et al. 1997, Friedlander and Parrish 1998, Friedlander 2001, Friedlander et al. 2003, Ferreira et al. 2004). Coral reefs in American Samoa were characterized by high

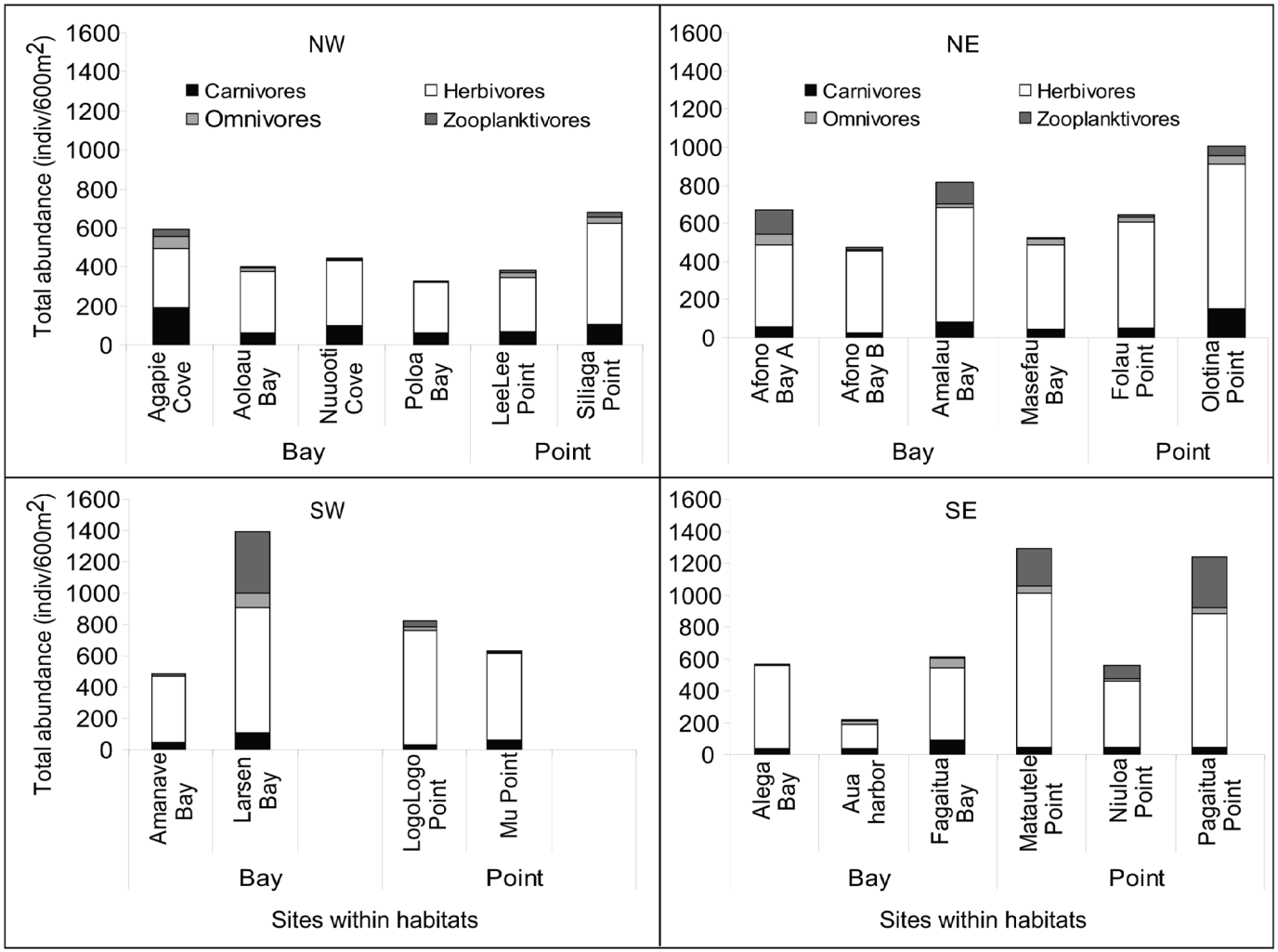

FIGURE 5. Total abundance of key reef species assigned to their respective trophic categories (carnivores, herbivores, omnivores, and zooplankton feeders) across sites nested within habitats and habitats within sector.

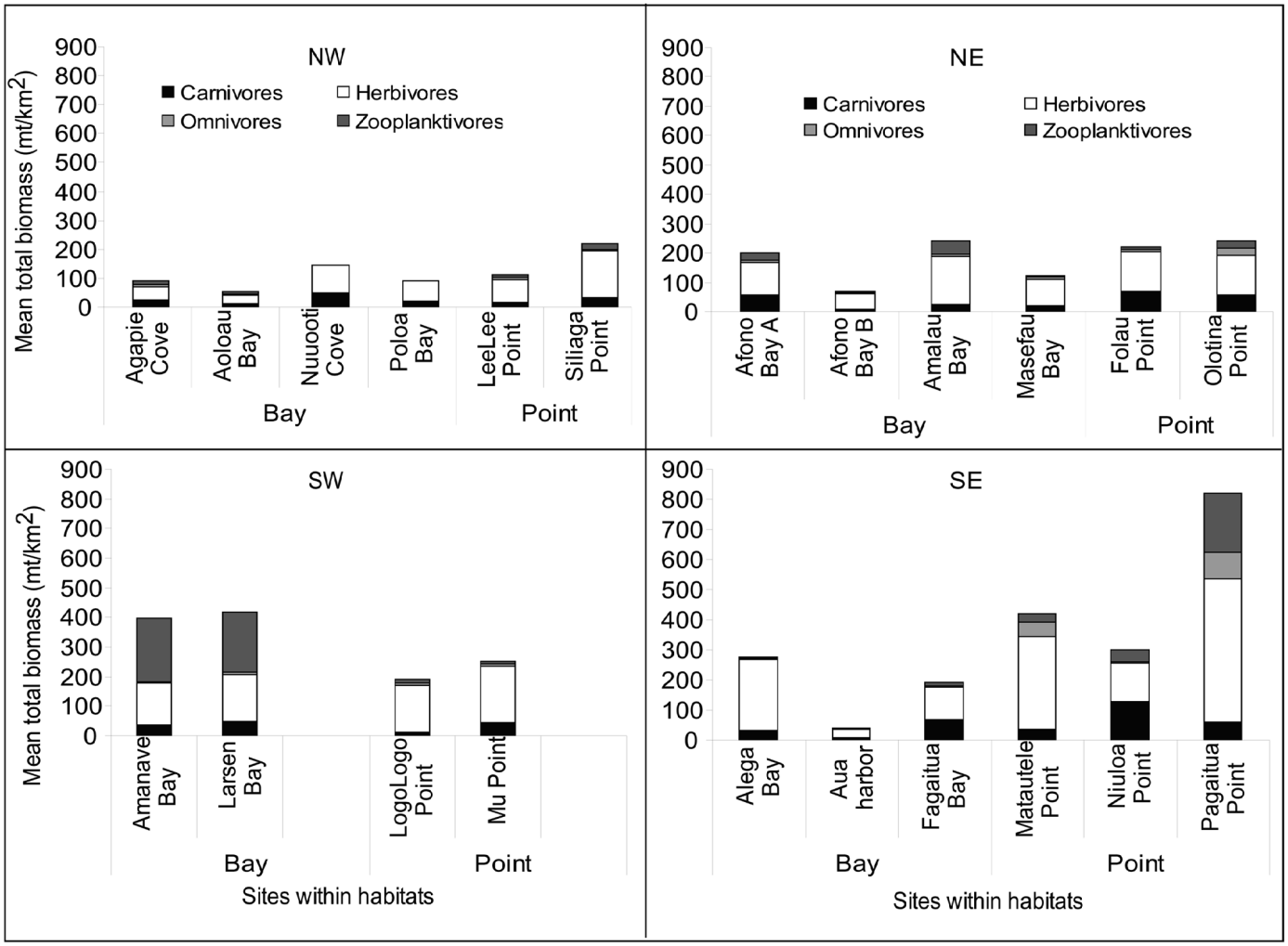

FIGURE 6. Mean of total biomass of key reef species assigned to their respective trophic categories (carnivores, herbivores, omnivores, and zooplankton feeders) across sites nested within habitats and habitats within sector.

TABLE 4

Multiple-Regression of Factor Scores of Carnivore Species and Benthic Cover

Species	Control Factor[a]	R	R^2	F (df = 1,81)	P
Live coral cover					
Plectropomus areolatus	LCC	0.266	0.071	6.186	.015
Lethrinus lentjan					
Variola louti					
Fleshy/filamentous and coralline algae cover					
Monotaxis grandoculis	FA	0.288	0.083	7.325	.008
Lutjanus monostigma	CA	0.227	0.052	4.399	.039
Aphareus rutilans					
Epibulus insidiator					

[a] LCC, live coral; FA, fleshy/filamentous algae; CA, coralline algae.

Note: Factor score was treated as the dependent variable and cover as the independent variable. Only significant species associations are shown.

TABLE 5

Multiple-Regression of Factor Scores of Herbivore Species and Benthic Cover

Species	Control Factor[a]	R	R^2	F (df = 1,81)	P
Fleshy/filamentous algae cover					
Scarus forsteni	FA	0.234	0.055	4.703	.033
Acanthurus olivaceus					
Scarus rivulatus		0.254	0.065	5.599	.020
Scarus niger					
Ctenochaetus striatus					
Chlorurus japanensis					
Acanthurus nigrofuscus		0.320	0.102	9.219	.003
Scarus oviceps					
Coralline algae cover					
Hipposcarus longiceps	CA	0.367	0.135	12.624	.001
Scarus ghobban					

[a] FA, fleshy/filamentous algae; CA, coralline algae.

Note: Factor score was treated as the dependent variable and cover as the independent variable. Only significant species associations are shown.

vertical relief, and pavement areas were considered less complex because of their flat surfaces (NOAA NCCOS 2005). Geographic Information System (GIS) mapping of coral reefs from satellite photos (NOAA NCCOS 2005) revealed more coral reef habitat along the southern shores of Tutuila, whereas benthic structures at the north shore were mostly volcanic pavement. A majority of the targeted fish assemblage in American Samoa can be characterized as generalist, with the dominant group (herbivores) being found in both habitat types and not strictly coupled with areas with high live coral cover. The higher fish biomass on the south shore of Tutuila is probably due to the greater extent of coral reef habitats there because of less disturbance from wave exposure. A similar pattern was reported by Green (2002), with higher mean fish biomass recorded on reefs located along the south shore. Habitat utilization was one major factor contributing to the distribution patterns of organisms (Garpe and Ohman 2003). The extent of habitat and not the quality was shown to be a driving factor for fish distribution in Mediterranean rocky reefs

(Garcia-Charton and Perez-Ruzafa 2001). Moreover, live coral cover was also shown to have very little effect on fish abundance in the Red Sea (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987), which supports our observation that the dominant group of fish (herbivores) does not have a strong association with live coral cover.

The dominance of herbivores in the reef fish community is typical in areas with a history of fishing activity (Friedlander and de Martini 2002, Friedlander et al. 2005). In contrast, in areas characterized by the absence of fishing (remote pristine areas or marine reserves closed for long periods), studies have shown dominance of larger carnivores (i.e., sharks and jacks) (Russ and Alcala 1996, 2003, 2004, Friedlander and de Martini 2002). The trophic patterns described in our study hold true only for the fringing reef areas in Tutuila Island at 10-m depth. American Samoa has several submerged banks and reefs that are yet unexplored and are the subject of current research.

Most villages are found within bay areas where fishing is most concentrated (Inshore Creel Data: Western Pacific Fisheries Information Network). The ocean condition on reefs located at geographic points is characterized by frequent large swells breaking at the crest, thus hindering fishing activities. This constrained fishing pressure could have led to higher numerical abundance and biomass at point areas than in bays. The presence of a fishing gradient alone, however, does not fully explain this spatial pattern because fishing continually has been decreasing in the past 25 yr (Coutures 2003). A recent survey showed that the majority of the population is not involved in subsistence, recreational, and commercial fishing, although some people still utilize the resources for cultural purposes (Kilarski et al. 2006). Other contributing factors such as environmental stress and nearshore habitat degradation may explain these variations, but this is as yet untested in American Samoa.

Spatial Patterns: Live Coral Cover across Scales

The spatial pattern in live coral cover is interesting because it showed a different pattern at the south than at the north shore. For the north shore, point areas had significantly less live coral cover than bays, but the reverse pattern occurred at the south shore. The reefs at the north shore are concentrated mostly in sheltered bays, and point areas are mostly volcanic pavements colonized by encrusting corals and coralline algae. Reefs may be underdeveloped at point areas due to strong wave action and storm surges originating far to the north. Wave exposure has been determined as a major inhibiting factor for reef development in Hawai'i, where most of the reefs are found in sheltered bay areas (Grigg 1983, 1998). The reefs at the south shore, however, are well developed, extending to point areas. Most of the waves from the south are generated by the trade winds and certain weather conditions (i.e., convergence) originating farther south. It is possible that wave intensity here is lessened due to dissipation of wave energy upon hitting Taema and Nafanua Banks. The southwest side of Tutuila also has a well-developed coral reef area because it is protected from the southeast trade winds.

Little variation in live coral cover was observed between transects within each site. This indicates that individual transects within a site are adequate to represent the site as a whole. Sites within a habitat, however, varied significantly due to heterogeneity in benthic assemblage at this scale. This implies that random site selection within a certain habitat is not enough to represent the whole habitat. This stochasticity in spatial distribution of live coral cover should be considered in various management strategies (Murdoch and Aronson 1999).

Spatial Patterns: Predator and Prey Relationship

We found significant associations between certain targeted species and the benthic composition. *Plectropomus areolatus*, *V. louti*, and *L. lentjan* were the species that had positive association with live coral cover. These are roving predators that feed mostly on fishes and are known to be highly associated with areas with high coral growth (Hiatt and Strasburg 1960, Masuda and Allen 1993). The effect of live coral cover could be direct where it provides fish habitat or indirect where it influences

the distribution of food sources of these species. The same pattern was observed with other carnivorous species, namely, *M. grandoculis*, *L. monostigma*, *A. rutilans*, and *E. insidiator* whose primary food items (gastropods, benthic crustaceans, ophiuroids, echinoids) were found in areas dominated by fleshy/filamentous algae and coralline algae. Macrozoobenthic assemblages have been shown to be abundant in areas with higher macroalgae cover (Kotta and Orav 2001) because dense macroalgae cover provides higher habitat complexity (Hardwick-Witman and Mathieson 1983).

Live coral cover, on the other hand, was not a significant factor for herbivore distribution. Herbivore distribution was associated with abundance of fleshy/filamentous algae and coralline algae. Distribution of herbivores has been shown to be correlated with abundance of their food items (Mateo and Tobias 2001). Herbivores, in turn, control the distribution and abundance of benthic species (Lewis 1986, Boaventura et al. 2002). Spatial patterns in herbivores are also controlled by interspecific interactions with other roving herbivores (Choat and Bellwood 1985). Feeding territories are known to be present in some species in which aggression or tolerance of other herbivores takes place. This is true for the reefs of American Samoa, where *Acanthurus lineatus*, *Stegastes nigricans*, and *Pomacentrus philippinus* were observed to form algal farms and aggressively defend their territory against some species and tolerate others (Craig 1996, Umezawa 2004).

CONCLUSIONS

Our results show that in spite of the small size of the island of Tutuila, there was significant spatial variation in abundance of the targeted species, with a majority of the differences occurring at the broadest spatial scales (habitat and exposure). These differences were brought about by the variations in habitat types, physical extent of habitats, and the level of association that each species has with the predominant benthic assemblage. Generalizations could be made at individual site levels within a habitat type, but extrapolation of biological data and patterns between habitat types could be erroneous. These results provide insights on how fish communities are structured by benthic communities and physical forcing functions.

Because biomass of targeted fishes differs at a habitat scale, and several fish species were shown to associate with various benthic components, this has some implications on how marine protected areas should be designed. Garcia-Charton and Perez-Ruzafa (1999) emphasized the use of multiscale analysis in describing different assemblages found within the area of interest and separating "reserve effects" from "habitat effects" by looking into various habitat types and levels of protection. They cautioned that a priori selection of the scale of protected areas could invalidate the conclusions due to anthropogenic biases of perception. Our study provides information on what scale is needed for marine protected areas (MPAs) to have a significant impact on targeted fish communities. We recommend setting up marine protected areas in American Samoa at a habitat scale (thousands of meters) instead of the customary site levels (hundreds of meters). Even if the targeted fish stocks are considered underutilized compared with stocks of neighboring South Pacific islands (Dalzell and Adams 1997, Page 1998, Coutures 2003), guaranteed perpetuation of these resources is crucial to the Samoan culture (Kilarski et al. 2006). Proper scaling of marine protected areas would ensure that factors influencing the distribution patterns of organisms and life history requirements are conserved so as to recover stocks and maintain biodiversity.

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